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COMMUNICATION, RAIDING BEHAVIOR AND PREY STORAGE IN *CERAPACHYS* (HYMENOPTERA; FORMICIDAE)*

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Introduction

The former subfamily Cerapachyinae was recently recognized by Brown (1975) as a tribe (Cerapachyini) within the subfamily Ponerinae. All of the cerapachyine ant species investigated feed entirely on ants (see review in Wilson 1958; Brown 1975). During foraging cerapachyine workers engage in mass expeditions during which they raid the nests of the prey species, capturing preferably larvae and pupae, but also occasionally adults and returning them to the raiders' nest.

Although the detailed field observations on cerapachyine foraging raids reported by Wilson (1958) strongly suggest that the raiding expeditions follow chemical trails, this has not yet been experimentally investigated. In fact, almost nothing was hitherto known about the behavioral organization of the raiding expeditions and the underlying communication mechanism. This paper presents the first experimental analysis of the raiding behavior of a cerapachyine ant species.

Materials and Methods

Three colonies of *Cerapachys (?) turneri* (turneri group) (accession #163a, b, c; voucher specimens in Australian National Insect

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Collection, ANIC, Canberra) were collected from nests in the soil in a sclerophyl scrub pasture near Eungella, North Queensland (Australia). One colony had a single ergatoid queen; the other colonies had two ergatoid queens apiece. Each colony was housed in separate glass tube nests (8 cm × 0.6 cm ϕ), with water trapped at the bottoms behind cotton plugs. Each nest tube was placed into arenas of varying sizes, depending on the experimental design. Histological studies were conducted according to the procedures described in Hölldobler and Engel 1978. Additional methodological details will be given with the description of the individual experiment, as presented below.

Results

Raiding behavior and paralysis of prey larvae

Species of the genus *Cerapachys* seem to preferably prey on ant species of the myrmicine genus *Pheidole* (Wilson 1958; Brown 1975). When I provided *Cerapachys* with colonies or fragments of colonies of a variety of species of the genera *Iridomyrmex, Meranoplus, Monomorium, Crematogaster, Pheidole, Stigmacros, Polyrhachis, Camponotus* (placed in a 65 × 120 cm arena) they preyed freely only on *Pheidole*. They also accepted *Monomorium* larvae as prey, but only when these insects were directly inserted into the *Cerapachys* nest. When the *Cerapachys* workers encountered workers of the other species, or came close to their nest tubes, they usually showed avoidance behavior. The reaction was very different, however, when individual scouts of *Cerapachys* discovered the nest tube of *Pheidole* (accession #209, voucher specimens in ANIC). The *Cerapachys* worker vigorously vibrated its short antennae and moved slowly into the nest tube, which contained approximately 200 *Pheidole* workers and soldiers and about 150 larvae and pupae. It did not venture very far into the foreign nest but left after a short while and ran, in a somewhat meandering route, back to its own nest, located 70 cm away from the *Pheidole* nest. During homing it appeared frequently to touch the ground with its abdominal tip, as if it were laying a chemical trail or depositing scent spots. Seconds after it had entered the nest of its own colony, its nestmates became very excited. Many grouped around the scout ant, which repeatedly raised its gaster upwards. Within one minute the scout left the nest

again and moved in direction toward the *Pheidole* nest tube. It was closely followed by 17 nestmates. The leading scout ant continued to move with its abdominal tip close to the ground, but intermittently it paused or moved much slower while raising its gaster slightly upwards (Fig. 1). When the *Cerapachys* column arrived at the *Pheidole* nest tube they invaded it and attacked the *Pheidole* workers and soldiers. *Pheidole* fought back but without any effect. The heavily sclerotized and specially protected *Cerapachys* (Fig. 2) were not at all affected by the mandibular grip of the *Pheidole* soldiers, even when they were attacked simultaneously by 3–5 *Pheidole* (Fig. 3). Although *Pheidole* outnumbered the *Cerapachys* invaders more than 10 times, they were rapidly disabled by the obviously very

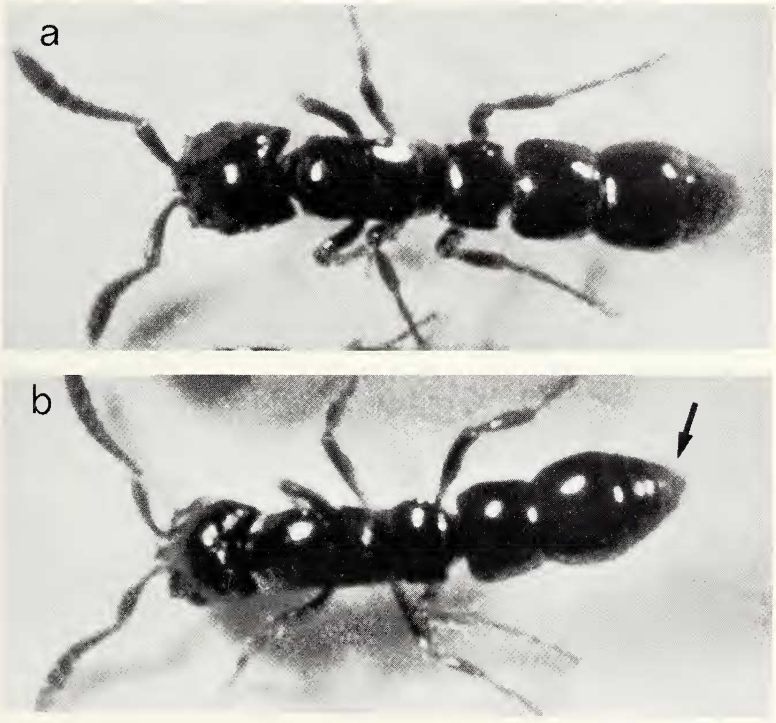

Figure 1. Recruiting *Cerapachys* worker. (a) Worker walking with its abdominal tip close to the ground. (b) Worker raising the gaster upwards; arrow indicates the position of the opening of the pygidial gland.

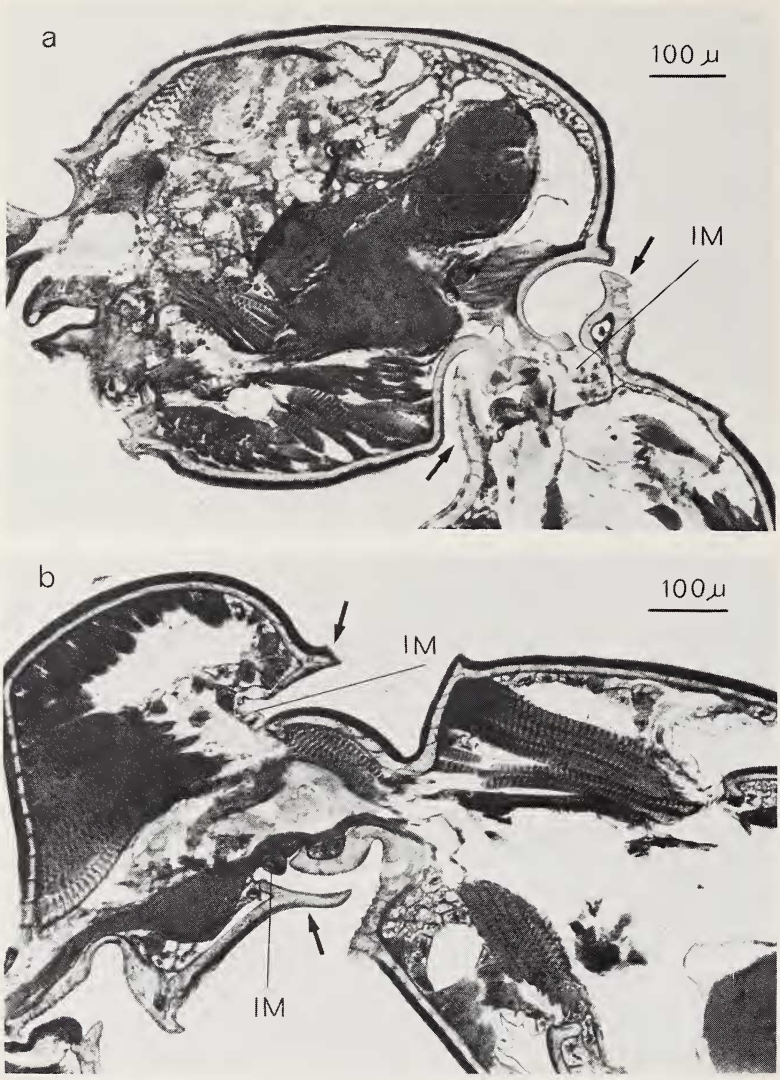

Figure 2. Longitudinal section through the head and part of the thorax (a) and through part of the petiolus and gaster (b) of a *Cerapachys* worker. Arrows indicate cuticle projections over intersegmental membranes (IM).

Figure 3. *Cerapachys* raiding group invading a *Pheidole* nest.

effective stinging attack of the *Cerapachys,* during which the raiders grasped the *Pheidole* with their short mandibles, simultaneously bending their gasters forward, so that in each case the tip, where the sting extrudes, touched the opponent's body. Each sequence usually lasted less than 1 second. Almost immediately after such an attack the *Pheidole* appeared to be immobilized. Only a few *Pheidole* workers escaped from the nest tube into the arena, some of them carrying brood. After approximately 15 minutes almost all *Pheidole* adults in the nest tube were disabled or killed but not a single *Cerapachys* worker was dead or visibly injured. Next the *Cerapachys* began transporting the dead and immobilized *Pheidole* adults to their own nest. After the first workers of the raiding expedition had returned and unloaded the booty they returned to the *Pheidole* nest. Some of them raised the gaster repeatedly upwards, upon which several additional *Cerapachys* workers followed them to the *Pheidole* nest, where they participated in the retrieval of the prey. Only after most of the *Pheidole* adults had been retrieved did the *Cerapachys* begin to transport the *Pheidole* brood. Each larva and pupa was briefly stung before it was picked up and carried to the *Cerapachys* colony. Interestingly, after approximately half the brood had been retrieved, *Cerapachys* nest workers began discarding all the dead and disabled *Pheidole* adults, and the next day only

Pheidole brood was stored in the *Cerapachys* nest. Apparently the booty of this raiding expedition was so abundant that *Cerapachys* preferred to keep only the more valuable and better preservable brood of the prey species, and they discarded the less valuable cadavers of the adult *Pheidole*. In other instances, however, where *Cerapachys* had only adults of prey species available, I observed *Cerapachys* feeding on the gasters of dead *Pheidole* workers and soldiers.

This experiment was conducted on the 25th and 26th of October 1980. At this time there was no *Cerapachys* brood in the colony. On November 10, 1980, I noticed the first large clutch of eggs in the *Cerapachys* nest tube. On December 11, 1980, the colony had many large (presumably last instar) larvae, and another large cluster of eggs (Fig. 4). The colony still contained a very good supply of *Pheidole* larvae (Fig. 4), which did not grow or develop further but which were obviously alive. Under the microscope one could see that the prey larvae slightly moved their mouthparts. Workers, queens and larvae of *Cerapachys* all fed on the *Pheidole* larvae. On December 26, 1980, there were still some prey larvae left. Many of the large *Cerapachys* larvae had pupated; in addition the nest contained many medium sized larvae and another large clutch of eggs. On January 3, 1981, a *Cerapachys* worker was observed leaving the nest tube and venturing out into the arena, for the first time since October 27, 1981. At this time I provided another fragment of a *Pheidole* colony with larval brood in the arena; and on January 5, 1981, *Cerapachys* conducted another raid, very similar in details to that just described. The fact that the captured *Pheidole* larvae were kept alive inside the *Cerapachys* nest chamber for a period of more than two months (but did not pupate or visibly increase in size) strongly suggested that they were sustained in a state of metabolic stasis. Recently Maschwitz et al (1979) provided experimental evidence that the ponerine species *Harpegnathus saltator* and *Leptogenys chinensis* paralize prey objects by stinging and thereby are able to store prey a limited time. In one case the preserving paralysis effect was observed to last for two weeks, and in no instance did the stung prey object ever recover from the paralysis. Similar observations have been made independently by Traniello (unpublished data) with the ponerine species *Amblyopone pallipes*.

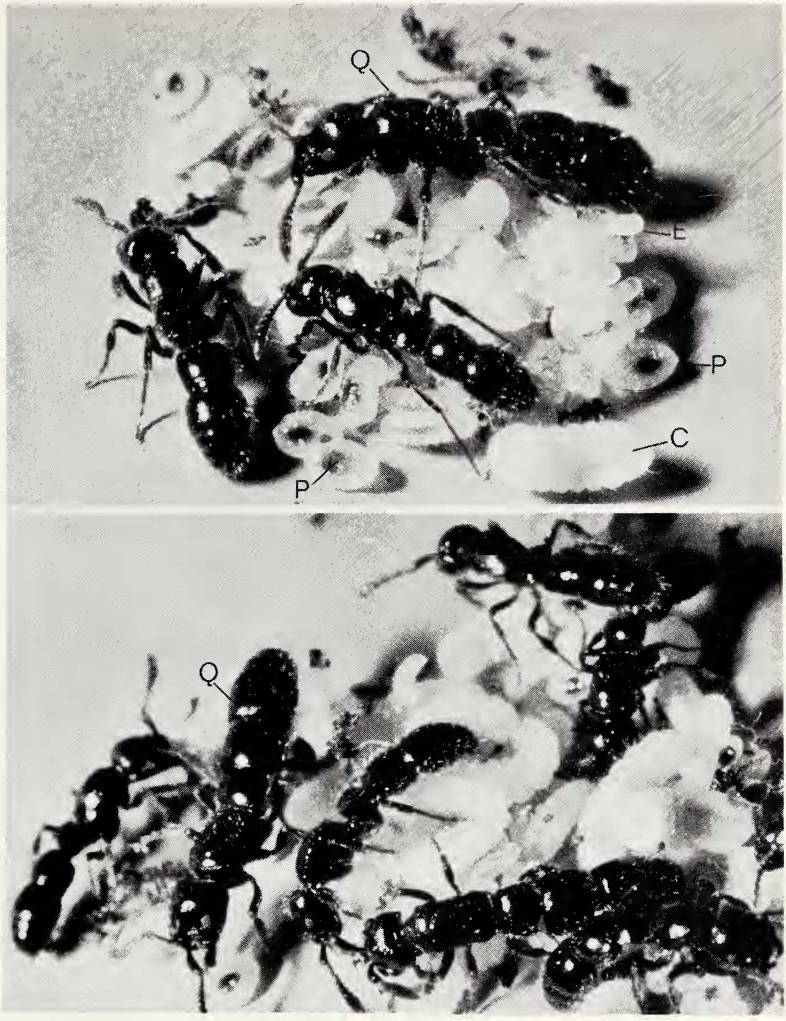

Figure 4. Fractions of a *Cerapachys* colony, with paralyzed prey larvae. Q: ergatoid queens; E: eggs; C: *Cerapachys* larvae; P: *Pheidole* prey larvae.

As just noted, *Cerapachys* workers apparently sting each *Pheidole* larva and pupa during the raid, before they transport the victims to their nest. This appears to be a very stereotyped behavior. For example when I shook a *Cerapachys* colony which contained *Pheidole* larvae out of the nest tube into the arena, so that they had to move back into the nest, *Cerapachys* workers picking up a *Pheidole* larva almost invariably went through the typical stinging motion pattern. They did not do this, however, when they picked up their own larvae. Although stinging behavior did not frequently occur inside the nest, occasionally I observed a *Cerapachys* stinging several larvae while reshuffling a pile.

The *Pheidole* larvae are small and tender and the powerful *Cerapachys* sting (Fig. 5) could easily pierce the larva and thereby kill it. Thus the injections of a paralyzing secretion through the sting has to be very subtle in order not to kill, but to preserve the larva. Brown (1975) describes the differentiated pygidium (Fig. 6) with its denticulate margins, being present in all workers and queens of cerapachyine ants. Brown states that "the function of the denticle-bordered pygidial plate is not known from direct observations, but it is assumed to have something to do with helping the insects to force their way through passages and cracks in soil or rotten wood, perhaps in connection with their entry into nests of termites or ant prey species".

Our morphological and histological investigations have revealed that these denticuliform and spinuliform setae on the pygidium of *Cerapachys turneri* and *Sphinctomyrmex steinheili* are sensory setae and comprise probably mechanoreceptors (Fig. 7). It is most likely that during the stinging process these mechanoreceptors signal the gaster tip's touch of the prey larva and the extent of the stings' protrusion is thereby regulated. Many of the nonsocial aculeate *Hymenoptera,* which paralyze prey by stinging, are equipped with mechanoreceptors on the tip of the sting sheath (Oeser 1961, Rathmayer 1962, 1978). We did not detect similar structures on the tip of the sting sheaths of *Cerapachys* or *Sphinctomyrmex.* In additional experiments I further confirmed the suggestion that the prey larvae, captured by *Cerapachys,* are preserved alive. Approximately 30 *Pheidole* larvae collected from a *Pheidole* colony were put without workers in a small test tube, which was kept moist by a wet cotton plug. A second similar test tube contained 30 *Pheidole* larvae which were taken from the *Cerapachys* nest. In two replications the

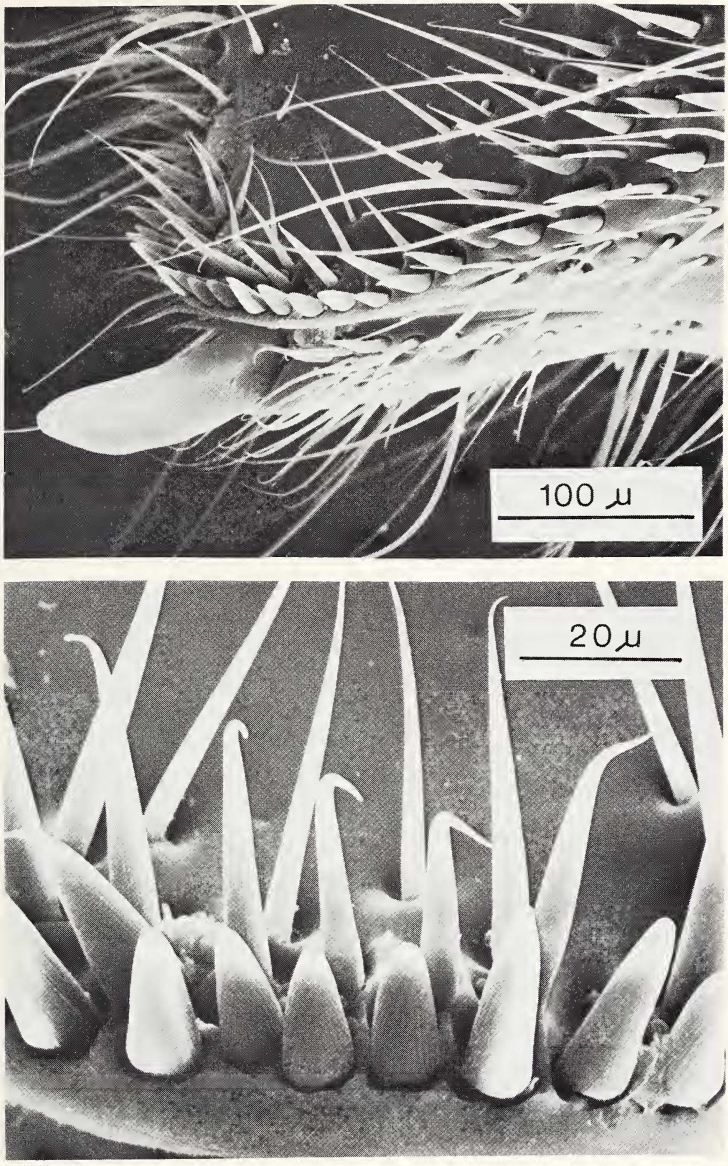

Figure 5. (a) SEM picture of the abdominal tip of a *Cerapachys* worker. The picture shows the partly extruded sting, surrounded by the sensory setae at the pygidium, and last exposed sternite. (b) Close-up of the two kinds of setae at the pygidium.

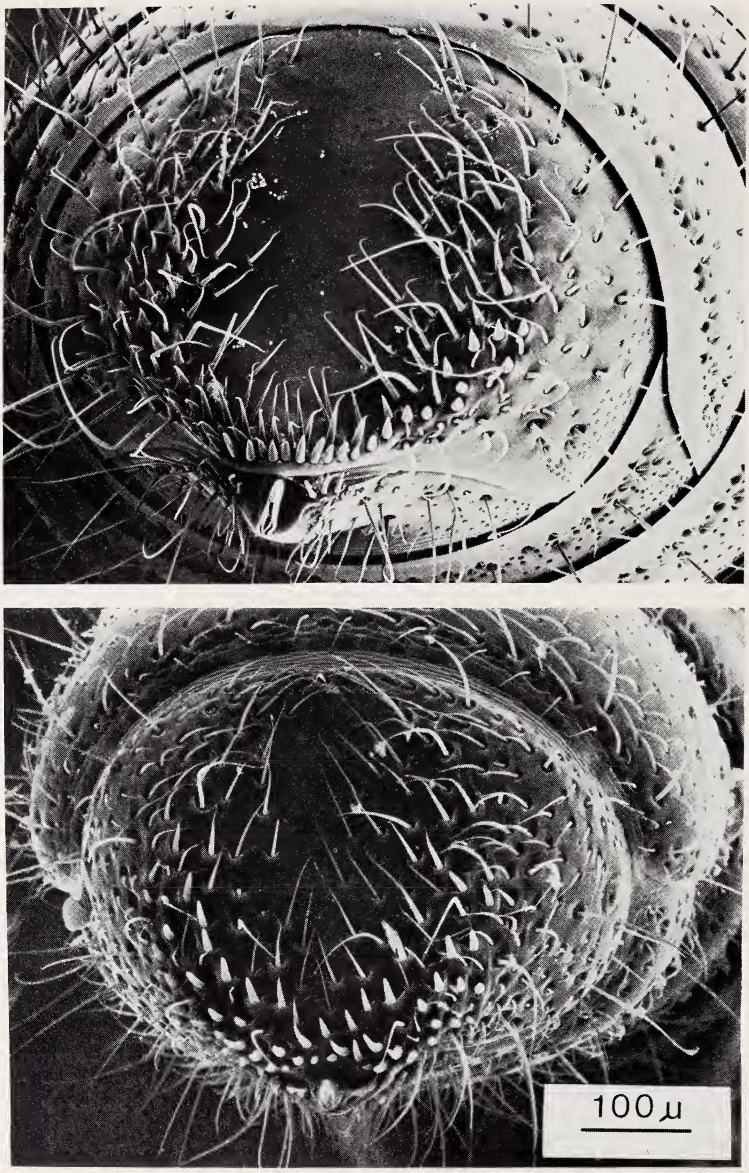

Figure 6. SEM picture of frontal view of pygidium of a *Cerapachys* worker (a), and a worker of *Sphinctomyrmex steinheili* (b). Note the arrangement of the two kinds of setae on the truncated pygidial plate of both species.

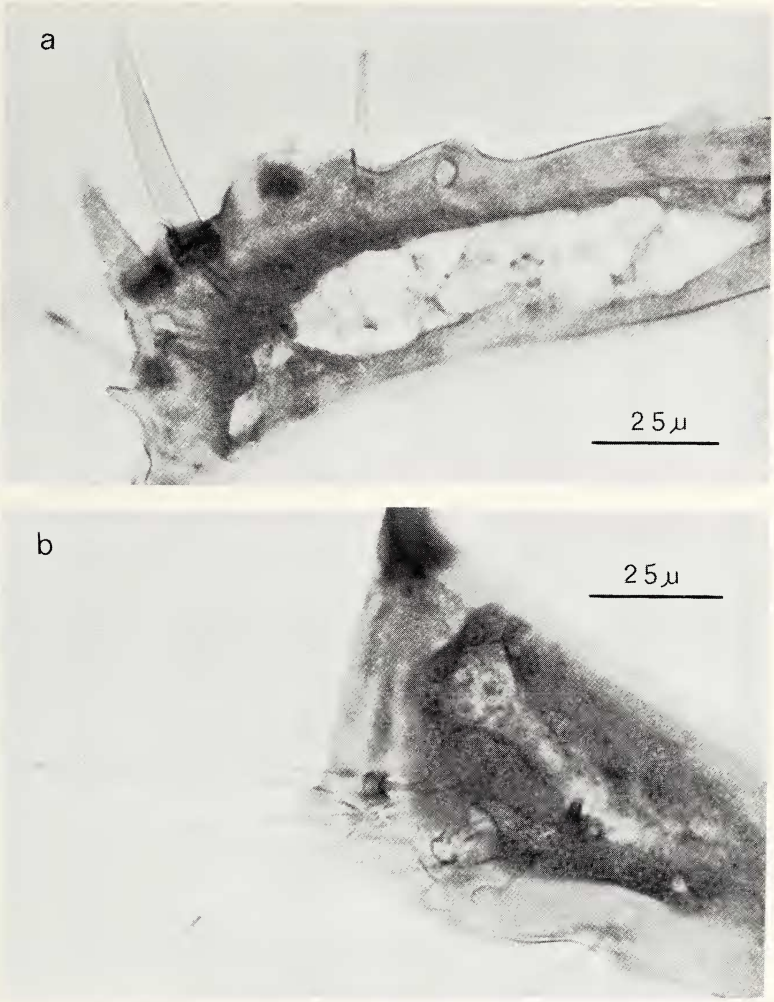

Figure 7. Longitudinal section through pygidial plate (a) and last exposed sternite (b) of a *Cerapachys* worker. The structure and innervation of the setae suggest that they function as mechano receptors.

larvae taken directly from the *Pheidole* colony were all dead after two weeks. On the other hand all of the larvae from the *Cerapachys* colony were obviously still alive after two weeks, many of them moving their mouthparts slightly. These findings clearly demonstrate that *Cerapachys* can store living prey larvae for a considerable period of time. This food storage system appears to enable *Cerapachys* to stay inside their nest for longer intervals. They evidently do not conduct raids as long as a good food supply is present. The following experiments were designed to test this hypothesis.

One day after the *Cerapachys* colony B had conducted a raid on *Pheidole* all prey larvae were removed. As a control I manipulated colony A in the same way, but the prey larvae were immediately returned to colony A. A few days later I observed scouts of colony B in the arena, where I had provided a nest tube with a fraction of a *Pheidole* colony, and within a period of 4 (test 1) and 7 days (test 2) colony B had conducted another raid. In the control colony A I noticed a worker briefly leaving the nest tube only once and then without venturing far into the arena. Although a tube containing *Pheidole* workers and brood was also provided in the arena of colony A, this colony did not conduct another raid until its supply of prey had declined considerably.

Emigration behavior

Although it is still an open question whether the Cerapachyini are nomadic, Wilson (1958, 1971) and Brown (1975) suggested that nomadism in the ant-preying cerapachyine species could well be adaptive to avoid depleting the food supply in a given neighborhood, just as it is in the army ants. This assumption of a nomadic life style is further supported by Brown's observations that the nests of many cerapachyine species appear to be impermanent, and that the "brood show a strong tendency to be synchronized, like those of army ants and nomadic Ponerinae". Brown (1975) also pointed out that the larvae of the Cerapachyini have a slender and cylindrical shape (G. C. Wheeler and J. Wheeler 1964), which makes them easy to transport longitudinally under the bodies of workers in the manner of other predatory and nomadic ants, such as *Eciton, Aenictus, Dorylus, Leptogenys* and *Onychomyrmex*. Although I was unable to demonstrate periodic nomadic behavior of *Cerapachys* in

the laboratory, I could easily initiate nest emigrations by removing the waterplug and thereby causing the nest tube to quickly dry out. Individual workers soon ventured into the arena and eventually discovered a new moist nest tube located approximately 20–30 cm away from the old nest. After exploring the new nest site the scout moved back to the colony. When entering the nest tube it exhibited the same behavior as when recruiting to a raid, including a repetitive lifting of the gaster. When the scout left the nest again to return to the newly discovered nest site, it was usually followed by several ants. Most of these first recruits also showed the gaster raising behavior on their return to the colony, and soon the whole colony began to leave the old nest tube and move to the new one. The larvae and pupae were carried in the manner Brown (1975) predicted, slung longitudinally under the bodies of the workers (Fig. 8). Adult transport was never observed; the ergatoid queens and even relatively freshly eclosed workers moved on their own to the nest site. The colonies did not contain males. After the workers had moved most of their own brood, they transported the prey larvae (*Pheidole*).

Figure 8. *Cerapachys* worker carrying a larva during nest emigration.

From the ants' orientation behavior it appeared that they were following chemical trails during the nest emigration. In fact, the recruitment behavior during nest emigrations and raiding appeared to be identical. The following experiments were designed to analyze further the communication mechanisms involved in both events.

Communication during emigration and raiding

Two distinct behavioral patterns were observed in *Cerapachys* ants during recruitment. (1) They seem to lay a chemical trail when returning from the target area (prey colony or new nest site) by frequently touching the abdominal tip to the ground; and (2) when close to or just entering the nest, they repeatedly raised their gaster upwards into a "calling position" and continued to do so when they moved back to the target area, usually being closely followed by a group of recruited nestmates. Since it was easier to initiate emigrations rather than raids, most of the experiments were conducted during colony emigration. Several new exocrine glandular structures have recently been discovered in ponerine ants (Hölldobler and Haskins 1977; Hölldobler and Engel 1978; Hölldobler et al. 1982; Maschwitz and Schönegge 1977; Jessen et al. 1979). The Cerapachyini were not included in these studies. We therefore conducted first a histological survey for possible exocrine glands that might be involved in the communication behavior of *Cerapachys*. Besides the known glands associated with the sting, we found a pygidial gland, which consists of a paired group of a few glandular cells under the 6th abdominal tergite. Each cell sends a duct through the intersegmental membrane between the 6th and 7th tergite (Fig. 9). The intersegmental membrane is laterally slightly invaginated, so that at each side it forms a small glandular reservoir. No particular cuticular structure on the pygidium is associated with the pygidial gland.

In a first set of pilot experiments I dissected out of freshly killed *Cerapachys* workers poison glands, Dufour's glands, hindguts, pygidial glands (6th and 7th tergites) and the last 3 sternites. For each test one organ of a kind was crushed on the tip of hardwood applicator sticks. These were then immediately inserted into the nest tube until the tip of the applicator was 2–3 cm away from the colony,

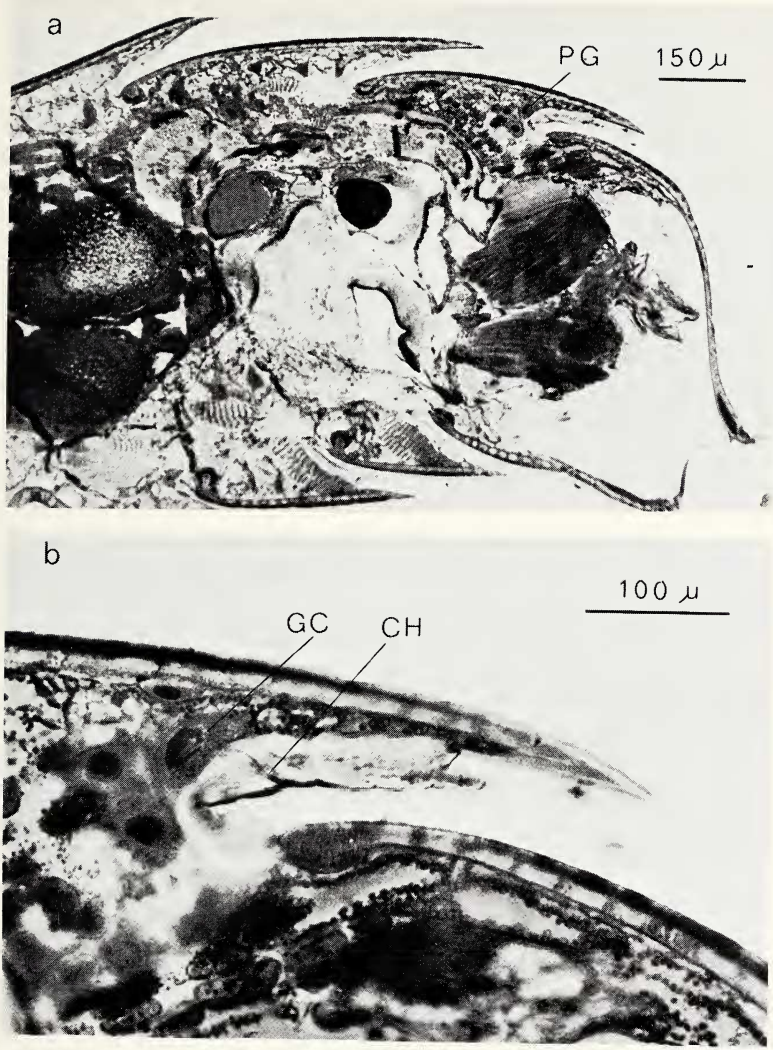

Figure 9. (a) Longitudinal section through the gaster of a *Cerapachys* worker showing the location of the pygidial gland (PG). (b) Longitudinal section through the pygidial gland; GC: glandular cells; CH: glandular channels through intersegmental membrane.

which usually had gathered near the cotton plug. In the following 30 seconds I observed the reaction of the ants, and between each test I waited at least 10 minutes before another sample was inserted into the nest tube. These pilot tests (3 repetitions with each organ) clearly indicated that only crushed poison glands and pygidial glands elicited increased locomotory activity and attraction in *Cerapachys* workers. The ants did not exhibit any particular behavioral reaction when sternites, hindgut or crushed Dufour's glands were introduced.* For the next series of experiments I first initiated colony emigrations either by following the procedure described above, or by shaking the colony out of the nest tube onto the arena floor. Before each experiment the arena was provided with a new paper floor. A new nest tube was offered 15-20cm away from the old nest tube or the displaced colony.

Once the colony emigration to the new nest tube had commenced, I covered the floor area between the colony and the new nest site with a cardboard, onto which I had drawn two artificial trails, one with a crushed glandular organ to be tested, and a second one with a drop of water (control). The trails were made to originate either from the entrance of the nest tube or from the periphery of the clustered colony. Each trail (test and control) diverged through an angle of 45° to either side from a possible natural trail (which was of course covered by a piece of cardboard). In addition the whole paper floor was rotated for 90°, in order to control for possible visual orientation (Fig. 10). During the following 2 minutes I counted the ants following the trails (10cm long) to the end. Only trails drawn with crushed poison glands elicited a precise trail following behavior in *Cerapachys* workers. There was some initial following response to trails drawn with crushed pygidial glands, but the ants followed only through the first 1–3cm, then usually turned or meandered off the trail. Only once was it possible to conduct a similar test during raiding behavior of *Cerapachys*. In this instance the ants followed only an artificial trail drawn with a crushed poison gland.

Although pygidial gland secretions did not release trail following behavior in *Cerapachys,* it clearly elicited increased locomotory

*_Cerapachys_ has also a very well developed sting sheath gland. It was not possible to test whether or not secretions of the gland play a role in communication.

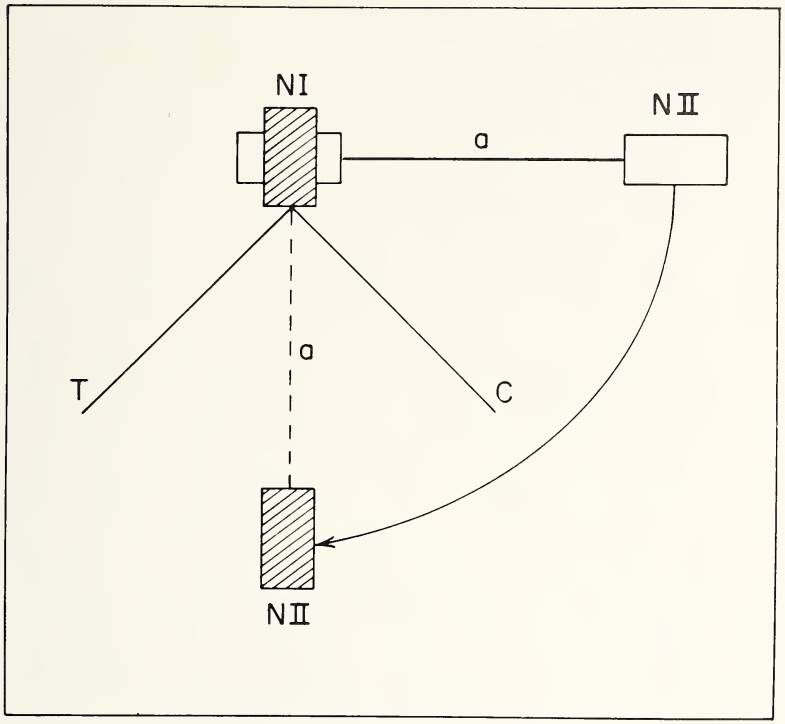

Figure 10. Schematical illustration of the experimental arrangement during trail tests. The colony was emigrating from nest NI to nest NII along a natural trail *a*. During the trail tests, the whole arrangement was turned 90° (arrow). The natural trail *a* was covered by a cardboard, on which the test trail (T) and a control trail (C) were offered, each deviating from *a* in an angle of 45°.

activity and attraction in the ants. I hypothesized therefore that the recruiting ant might discharge pygidial gland secretions when it exhibited the gaster raising behavior. The pygidial gland pheromone might function as an additional recruitment signal by which the recruiting ant keeps the raiding party stimulated when leading it to the prey colony. In order to test this hypothesis, I tried on four different occasions to close the opening of the pygidial gland by applying collophonium wax between the 6th and 7th tergites. Unfortunately these experiments failed; apparently the ants were too disturbed by the procedure. During two raiding expeditions of

Cerapachys we succeeded, however, in diverting individual ants from the raiding column over a distance of at least several centimeters by presenting two applicators in front of them, one contaminated with pygidial gland secretions and the other with water. Both applicators were slowly moved away from the columns in opposing directions. Of a total of 10 ants tested, 4 responded by following for a few centimeters behind the applicator with the pygidial gland secretions; no ant followed the control applicator. Although these results can be considered only preliminary, they do suggest that pygidial gland secretions might be involved in the recruitment process of *Cerapachys*. This suggestion was further supported by the results of a series of experiments in which I offered artificial trails drawn with crushed poison glands. I compared the trail following response of *Cerapachys* (within the first two minutes) successively either to trails drawn with poison gland secretions only or to poison gland trails offered simultaneously with pygidial gland secretions. For each kind a total of 6 experiments was carried out. Between each test at least one day had elapsed. The following response appeared to be stronger to poison gland trails when offered together with pygidial gland secretions (5.5 ± 2.9) than to those offered without pygidial gland secretions (3.0 ± 1.4) ($0.1 > p > 0.05$; Students t-test). Because of lack of material this series could not be extended, and thus the results remain only suggestive.

The two final experiments demonstrated that a trail (10 cm long) drawn with one crushed poison gland, was still effective as an orientation cue several hours after it had been drawn. Using the same experimental arrangement described above (Fig. 10), I was able to show that emigrating *Cerapachys* would follow poison gland trails, 2 and 6 hours old, when they were offered after the natural trail had been covered. On the other hand, crushed poison glands introduced into the nest tube after 2 and 6 hours, or poison gland trails offered 2 and 6 hours after they had been drawn, did not elicit excitement or spontaneous trail following behavior. From these results it appears that the poison gland material might contain a short lasting stimulating component as well as a longer lasting orienting component.

Discussion

Raiding expeditions in *Cerapachys turneri* are organized by individual scout ants, that return to the colony after having discovered a nest of the prey species. The scout lays a chemical trail with secretions from the poison gland, which serve as recruitment and orientation signals for the nestmates. Circumstantial evidence suggests that in addition the scout releases a stimulating chemical recruitment signal from the pygidial gland. This occurs probably when the scouts move with their gaster held slightly upwards in a calling position.

Wilson (1958) reports the field notes made by H. Potter on the cerapachyine species *Phyracaces potteri,* which contain the only available description of the early stages of a complete raid observed in the field. Before the raid started Potter noted a few workers moving rapidly about, "each with its abdomen raised upwards". These observations match closely my findings in the laboratory and lend further support to the hypothesis that in addition to the trails laid with poison gland secretions, another stimulating signal is discharged, presumably from the pygidial gland of the recruiting ants.

Wilson (1958) observed groups of *Phyracaces* moving along a raiding trail laid down by a raiding party on the previous day. In this case no individual leadership was involved and the foragers seemed to emerge from the nest randomly without a special recruitment stimulation by scout ants. Obviously these ants were following an established foraging trail, leading to a previously raided *Pheidole* nest which appeared to be vacated this time. Small exploratory parties conducted brief excursions to the side, but in most cases they turned back to the main trail. No nest suitable for raiding was found during these explorations.

These observations strongly suggest that chemical trails laid during raiding expeditions might still function as orientation cues one day later and that foraging parties can follow these established trails without the leadership of a recruiting scout ant. Indeed, my laboratory experiments with *Cerapachys* have demonstrated that artificial trails drawn with poison gland material are effective as orientation cues at least for several hours.

Although the raiding cerapachyine ants are usually enormously outnumbered by the worker force of the prey species, not one *Cerapachys* worker was lost during all the raiding experiments in the laboratory. As can be seen from Fig. 2, *Cerapachys* and *Sphinctomyrmex* are excellently protected by a heavily sclerotized cuticle. The intersegmental joints, that is, the joints between head and thorax, and between thorax, petiole and gaster, are covered by cuticular projections so that no intersegmental membrane is exposed, even if the ant is twisted and bent to an extreme degree.

In addition, *Cerapachys* and probably all the other cerapachyine ants have a most powerful sting that immobilizes the opponents within seconds. Not only the adults of the raided colony, but also the captured larvae and pupae are stung by the raiders before they are retrieved to the *Cerapachys* nest. Observations and experiments demonstrated that the prey larvae are kept in a stage of metabolic stasis and can thereby be stored for a period of more than two months. This food storage system enables *Cerapachys* to adjust the raiding activities to food requirement and supply. From the laboratory experiments we can conclude that *Cerapachys* does not conduct daily or periodic raiding expeditions. The frequency of raiding expeditions depends on the food supply stored inside the *Cerapachys* nest.

I was unable to demonstrate periodic nomadic behavior in *Cerapachys* in the laboratory. I assume that nest emigrations might occur relatively frequently in this species, but that they do not follow a periodic pattern. Instead, environmental factors such as food supply or physical conditions of the nest site are likely to play the important role in inducing a *Cerapachys* colony to emigrate.

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